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FIVE NEW SPECIES OF *CHROMODORIS* (MOLLUSCA:
NUDIBRANCHIA: CHROMODORIDIDAE) FROM THE
TROPICAL INDO-PACIFIC OCEAN

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Five new species of *Chromodoris* are described from the tropical Indo-Pacific. Three of these, *Chromodoris joshi*, *C. diana* and *C. michaeli*, are members of the *Chromodoris quadricolor* complex. *Chromodoris joshi* is known from the Philippines, Indonesia and the Andaman Sea, Thailand. *Chromodoris diana* is commonly found in the Philippines, Indonesia and Malaysia. *Chromodoris michaeli* is known from the Philippine Islands of Luzon, Cebu and Mindanao. *Chromodoris hintuanensis* is known from the Ryukyu Islands, the Philippines, Indonesia, Papua New Guinea and Thailand. It is compared to two similar species, *C. geometrica* and *C. conchyliata*. *Chromodoris roboi* is known from the Ryukyu Islands and Lord Howe Island and Western Australia and is similar in color pattern to *C. vibrata* and *C. aureopurpurea*. Consistent patterns of radular morphology, mantle gland arrangement and reproductive anatomy suggest that members of the *Chromodoris quadricolor* complex may be closely related phylogenetically in addition to having a similar color pattern.

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Numerous species of the highly diverse nudibranch genus *Chromodoris* have been recently described from many localities in the tropical Indo-Pacific (Rudman 1977, 1982, 1983, 1984, 1986, 1987; Yonow 1994; Gosliner 1994). Our recent field collections in the Philippines as well as collections and observations by others from Indonesia, Papua New Guinea, Okinawa, Malaysia and Thailand have yielded specimens of several new species of *Chromodoris*. This paper describes five of these new species and provides comparison with other species that are similar in appearance.

In several of Rudman's papers he has dealt with different color groups of chromodorids. In

his 1977 and 1982 works, he has described several species with black lines which he included in the *Chromodoris quadricolor* complex. Three of the new species described here are members of this complex. The other two are similar to members of two other color groups of chromodorids.

SPECIES DESCRIPTIONS

***Chromodoris joshi* sp. nov.**
(Figs. 1A, 2A–D, 3A–D, 4A)

Chromodoris sp. Debelius, 1996:213, top photograph.

Chromodoris quadricolor Dakin, 1992:346, bottom photograph, not (Rüppell and Leuckart, 1828), misidentification.

TYPE MATERIAL. — Holotype: CASIZ 083806, one specimen, Kirby's Rock, Caban Island, Maricaban Strait, Philippine Islands, 24 February 1992, Jerry Allen. Paratypes: CASIZ 083674, two specimens, Sepok Point, SW side Maricaban Island, Philippine Islands, 15 m depth, 19 February 1992, T. M. Gosliner. CASIZ 096328, two specimens, Sepok Point, SW side Maricaban Island, Philippine Islands, 20 m depth, 17 March 1994, T. M. Gosliner and M. Miller. CASIZ 105711, one specimen, Anilao, Batangas Province, Luzon, Philippine Islands, M. Miller. CASIZ 103750, two specimens, one dissected, Pinnacle Rock, Hamilo Bay, Luzon, Philippine Islands, 10 m depth, 4 March 1995, Michael T. Ghiselin. CASIZ 105641, two specimens, Escarcia Point, Sabang, Mindoro, Philippine Islands, 14 m depth, 1 March 1995, T. M. Gosliner. CASIZ 085974, one specimen, Cathedral Rocks, Balayan Bay, Luzon, Philippine Islands, 20 m depth, 25 March 1993, T. M. Gosliner. CASIZ 110468, one specimen, buccal mass removed, Philippine Islands.

ETYMOLOGY. — *Chromodoris joshi* is named for the first author's son, Joshua Todd Gosliner, a bright enthusiastic student, who has had to put up with several missed birthdays while his father was conducting field work in the Philippines.

DISTRIBUTION. — Thus far, this species is known only from the Philippine Islands (present study), from a photograph by Jim Black from Sumatra, Indonesia (Debelius 1996), and from photographs by Mark Strickland of a specimen found in the Andaman Sea, Thailand.

NATURAL HISTORY. — *Chromodoris joshi* is found on the outer edges of rock walls and reef fronts in 5–30 meters of water.

EXTERNAL MORPHOLOGY. — Preserved animals are 22–60 mm in length. The living animals (Fig. 1A) are buttery yellow with a darker, golden yellow margin. White flecks are scattered densely within the yellow pigmented areas. A wide, black, submarginal band encircles the dorsal surface of the animal, from the anterior end of the notum to a short distance behind the gill

plume. The band is somewhat variable in width between specimens and in one specimen the band is much wider at the middle of the animal creating an hourglass effect. The band may also appear as two narrower bands along the sides of the body in some animals where the black is broken with a narrow gray area. A black stripe of about the same width begins anteriorly at or just behind the submarginal band and runs longitudinally between the rhinophores down the midline of the animal (Figs. 1A and 2A). The stripe may extend to near the base of the gill pocket but in one animal the stripe terminates before the midline of the body. The stripe may be discontinuous in places. The black color fades to gray along the edges of the bands. In all specimens seen, gills and rhinophores are uniformly pumpkin yellow-orange. The gills of the specimen figured by Debelius (1966:213) are orange basally, while the upper two-thirds are white. The triangular foot is the same color as the body and extends posteriorly beyond the notum. Two black stripes run along either side of the dorsal surface of the foot. The mantle glands (Fig. 2B, 4A) are continuous around the margin of the notum except for the anterior portion of the animal from just behind the rhinophores where they are absent. The glands consist of spherical lobes that are clustered together closely resembling bunches of grapes (Fig. 2C). On either side of the head is a short, digitiform tentacle. There are 11–15 unipinnate gills forming the branchial plume. The perfoliate rhinophores bear about 30 lamellae.

BUCCAL ARMATURE. — The muscular portion of the buccal mass is approximately equal in length to the oral tube. At the anterior end of the muscular portion of the buccal mass is the chitinous labial cuticle, which bears numerous jaw rodlets. The rodlets (Fig. 3A) are elongate, curved and mostly undivided at the apex while a few are bifid in one specimen (CASIZ 110468). The radular formula is $81 \times 96.0.96$ in one specimen examined (CASIZ 103750) and $103 \times 90.0.90$ in a second specimen (CASIZ 110468). There is no trace of a rachidian tooth. The inner-

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FIGURE 1. Living animals. A. *Chromodoris joshi* sp. nov., specimen from Sepok Point, NW side Maricaban Island, Philippine Islands, photograph by T. M. Gosliner. B. *Chromodoris diana* sp. nov., specimen from Batangas, Philippine Islands, photograph by Mike Miller. C. *Chromodoris diana* sp. nov., specimen from Kirby's Rock, Caban Island, Maricaban Strait, Philippine Islands, photograph by T. M. Gosliner.



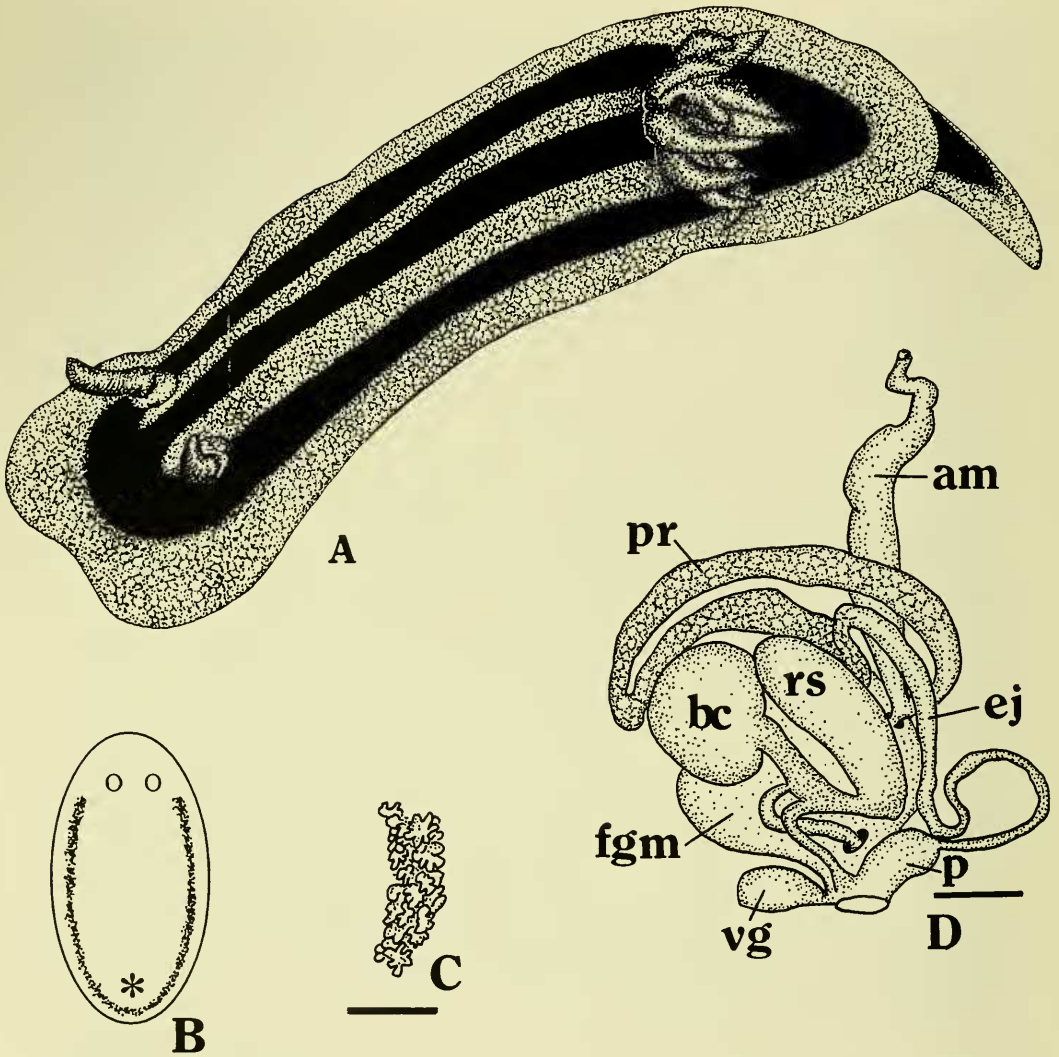


FIGURE 2. *Chromodoris joshi* sp. nov. A. Living animal. B. Subcutaneous glandular network. C. Mantle glands, enlarged, scale = 1.0 mm. D. Reproductive system, am = ampulla, bc = bursa copulatrix, ej = ejaculatory duct, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, vg = vestibular gland, scale = 1.0 mm.

most lateral teeth (Fig. 3B) are arched with a short cusp. There are 0–4 poorly-developed denticles on the inner side of the tooth. The outer side lacks denticles. The second through fourth lateral teeth entirely lack denticles. The lateral teeth from the middle of the radular row (Fig. 3C) bear 1–5 minute, triangular denticles on the outer side of the teeth. The outermost lateral teeth (Fig. 3D) are elongate with one to four denticles.

REPRODUCTIVE SYSTEM. — (Fig. 2D) The ampulla is thick and tubular, narrowing somewhat before bifurcating into an oviduct and vas

deferens. The short oviduct enters the female gland mass near the albumen gland. The proximal prostatic portion of the vas deferens is folded over itself once before it narrows slightly into the relatively short, muscular, ejaculatory portion. The ejaculatory portion narrows abruptly to a curved segment and then enters the short penial bulb, which is adjacent to the slender vaginal duct at the common gonopore. The distal end of the vas deferens is devoid of any penial hooks. The female gland mass consists of the large mucous gland and smaller membrane and albumen

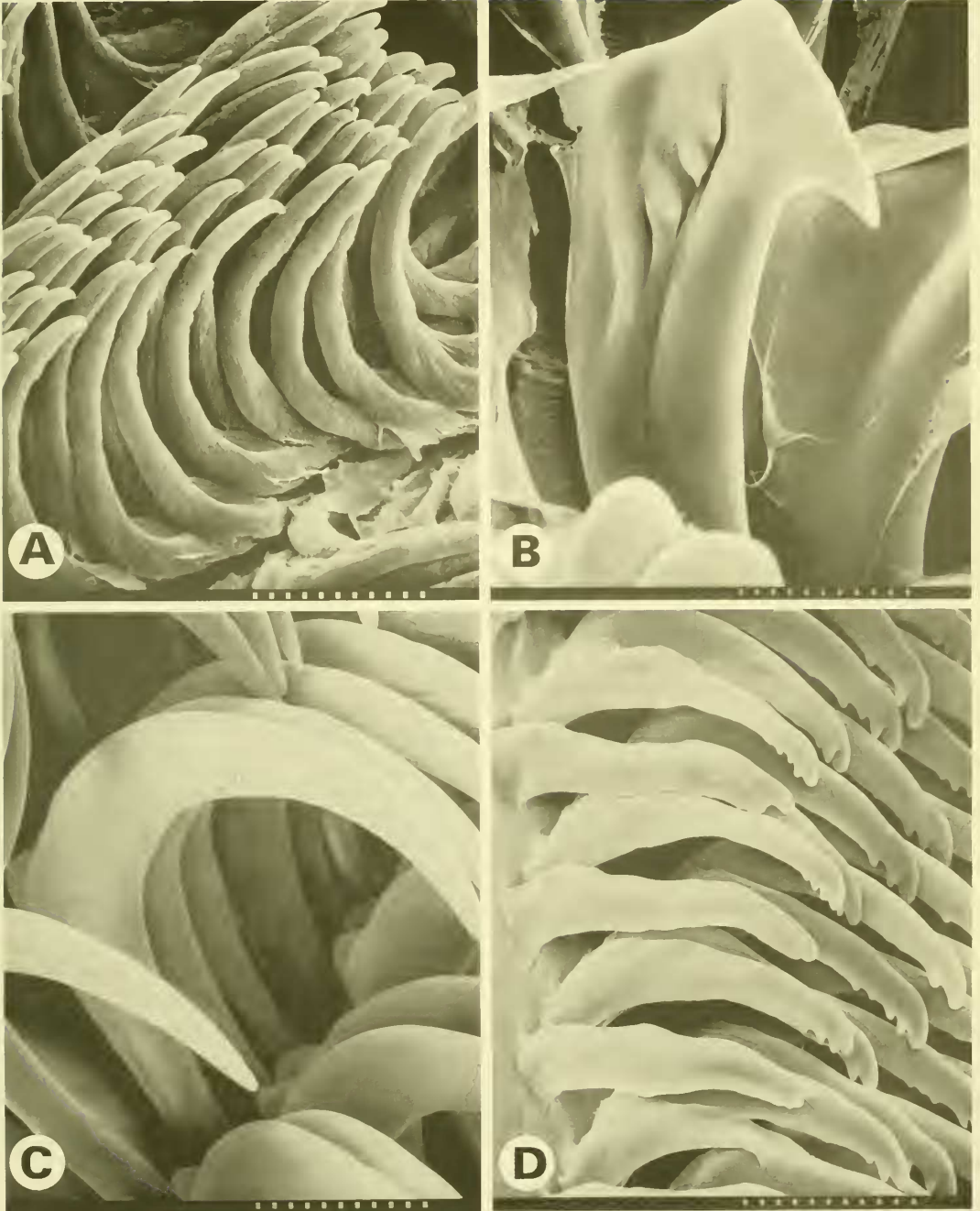


FIGURE 3. *Chromodoris joshi* sp. nov. Scanning electron micrographs. A. Jaw rodlets, scale = 15 μ m. B. Inner lateral teeth, scale = 15 μ m. C. Lateral teeth from central portion of half-row, scale = 25 μ m. D. Outer lateral teeth, scale = 43 μ m.

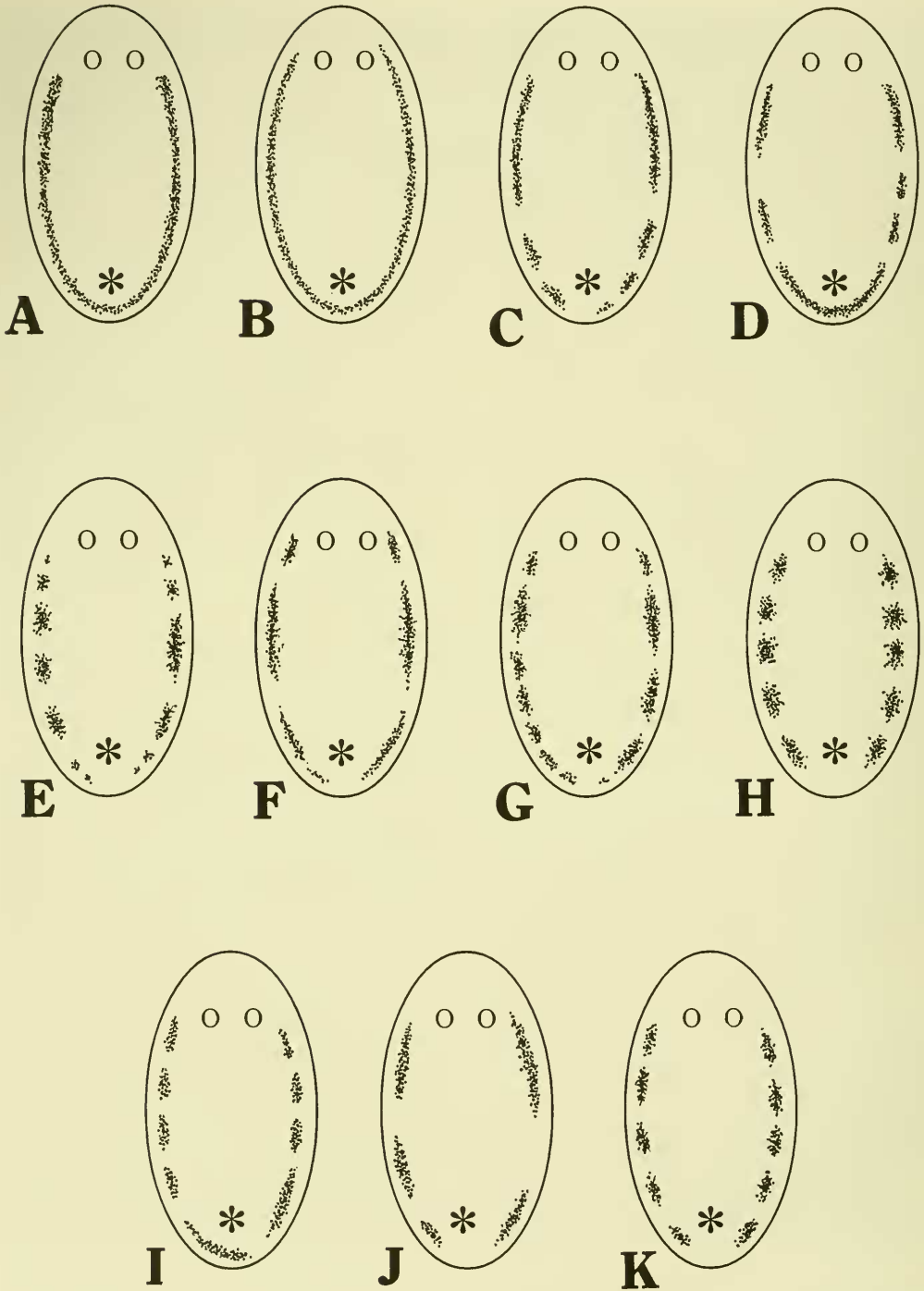


FIGURE 4. Mantle gland distribution. A. *Chromodoris joshi* sp. nov. B. *C. africana* Eliot, 1904. C. *C. magnifica* (Quoy and Gaimard, 1832). D. *C. strigata* Rudman, 1982. E. *C. diana*e sp. nov. F. *C. lochi* Rudman, 1982. G. *C. willani* Rudman, 1982. H. *C. elisabethina* Bergh, 1877. I. *C. michaeli* sp. nov. J. *C. annae* Bergh, 1877. K. *C. hamiltoni* Rudman, 1977.

glands. Near the exit of the mucous gland is a small, ovoid vestibular gland. The vagina is relatively short. At the proximal end of the vagina is a short duct to the club shaped receptaculum seminis and a long, wide duct to the thin walled, spherical bursa copulatrix. The uterine duct emerges at a position one third of the length along the duct leading to the bursa and enters the female gland mass near the albumen gland.

DISCUSSION. — *Chromodoris joshi* is most similar in external appearance to other members of the *Chromodoris quadricolor* complex that have prominent black mantle coloration, namely *C. africana* Eliot, 1904, *C. magnifica* (Quoy and Gaimard, 1832), and *C. kuiteri* Rudman, 1982. However, *C. joshi* lacks an orange marginal mantle band and has yellow rather than white pigment in addition to the black. Among these four species, the mantle glands are similar to those observed in *C. africana* and *C. magnifica* (Figs. 4B, C, respectively). The glands of *C. joshi* and *C. africana* are closely crowded in a continuous array, while in *C. magnifica* groups of glands are somewhat isolated, especially in the posterior region of the mantle. The mantle glands are not described for *C. kuiteri*.

There are significant differences in the buccal armature among the four darkly-pigmented species. In *C. joshi*, a majority of the jaw rodlets are unifid, while in *C. africana*, *C. kuiteri* and *C. magnifica* the rodlets are bifid (Rudman 1977, fig. 18C; Rudman 1982). The denticulation of the radular teeth varies between species. In *C. kuiteri* and *C. magnifica* all of the radular teeth have denticles on their outer side and a vestigial, triangular rachidian tooth is present. In *C. joshi* and *C. africana* there is no vestige of a rachidian and the inner lateral teeth lack denticles on the outer side. In *C. joshi* the next three teeth lack denticles. From tooth five to the outer edge of the radula minute denticles are present on the outer side of the tooth. In *C. africana*, the first 30 teeth lack denticles on the outer side while the remaining teeth have a few small denticles.

The reproductive systems of *C. magnifica* and *C. africana* were described and illustrated by Rudman (1977, figs. 17A, C). In both of these species the vagina and the ejaculatory portion of the vas deferens are much shorter than in *C. joshi*. In *C. joshi* the ejaculatory segment consists of a wide proximal portion and a much thinner distal one, while in the above two species it appears to

be of a uniform diameter throughout its length. The arrangement of reproductive organs of *C. joshi* is very similar to that described for *C. kuiteri* (Rudman 1984:137, fig. 13B).

***Chromodoris diana* sp. nov.**
(Figs. 1B, C; 4E; 5A–D; 6; 7A–D)

Casella sp. Wong, 1991:103.

Chromodoris sp. Allen and Steene, 1994:198, photograph in second row, first column.

Chromodoris sp. Colin and Arneson, 1995:183, figs. 852 and 856.

TYPE MATERIAL. — Holotype: CASIZ 106464, one specimen, Arthur's Rock, Calumpán Peninsula, Luzon, Philippine Islands, 17 April 1996, Jerry Allen. Paratypes: CASIZ 083686, three specimens, one dissected, Kirby's Rock, Maricaban Island, Philippine Islands, 23 m depth, 18 February 1992, T. M. Gosliner. CASIZ 103789, two specimens, Cathedral Rock, Batangas Province, Luzon, Philippine Islands, 22 m depth, 25 February 1995, T. M. Gosliner. CASIZ 086002, three specimens, N end of Ligo Island, Balayan Bay, Luzon, Philippine Islands, 26 m depth, 24 March 1993, T. M. Gosliner. CASIZ 084276, eight specimens, N end of Ligo Island, Balayan Bay, Luzon, Philippine Islands, 21 m depth, 25 February 1992, T. M. Gosliner. CASIZ 076326, one specimen, SW corner of north reef, Tubbataha Reefs, Sulu Sea, Philippine Islands, 9°09'N, 119°55'E, 8–16 m depth, 13 March 1984, Antonio J. Ferreira. CASIZ 096278, three specimens, Kirby's Rock, Caban Island, Maricaban Strait, Philippine Islands, 18 m depth, 17 March 1994, T. M. Gosliner. CASIZ 084292, one specimen, Bus Stop Reef, Balayan Bay, Luzon, Philippine Islands, 23 m depth, 21 February 1992, T. M. Gosliner. CASIZ 087270, one specimen, Manado, Celebes Sea, Sulawesi, Indonesia, April 1988, Pauline Fiene-Severns. CASIZ 096266, three specimens, Kirby's Rock, Caban Island, Maricaban Strait, Philippine Islands, 25 m depth, 13 March 1994, T. M. Gosliner. CASIZ 076308, three specimens, Jessie Beazley Reef, Tubbataha Reefs, Sulu Sea, Philippine Islands, 2–77 m depth, 9°02'N, 119°49'E, 15 March 1984, Antonio J. Ferreira. CASIZ 076288, three specimens, Filomona Shoals, Coyos Island, Sulu Sea, Philippine Islands, 10°40'N, 120°46'E, 25–33 m depth, 10 March 1984, Antonio J. Ferreira. CASIZ 076374, one specimen, Ilin Point, Ilin Island, off Mindoro, Philippine Islands, 16–23 m depth, 17 March 1984, Antonio J. Ferreira. CASIZ 110465, one specimen, Kirby's Rock, Caban Island, Maricaban Strait, Philippine Islands, 25 m depth, 19 April 1997, D. W. Behrens. CASIZ 110466, one specimen, buccal mass removed, Santa Rosa Island, Cebu, Philippine Islands, 20 m depth, 27 April 1997, Nora Ross. CASIZ 110467,

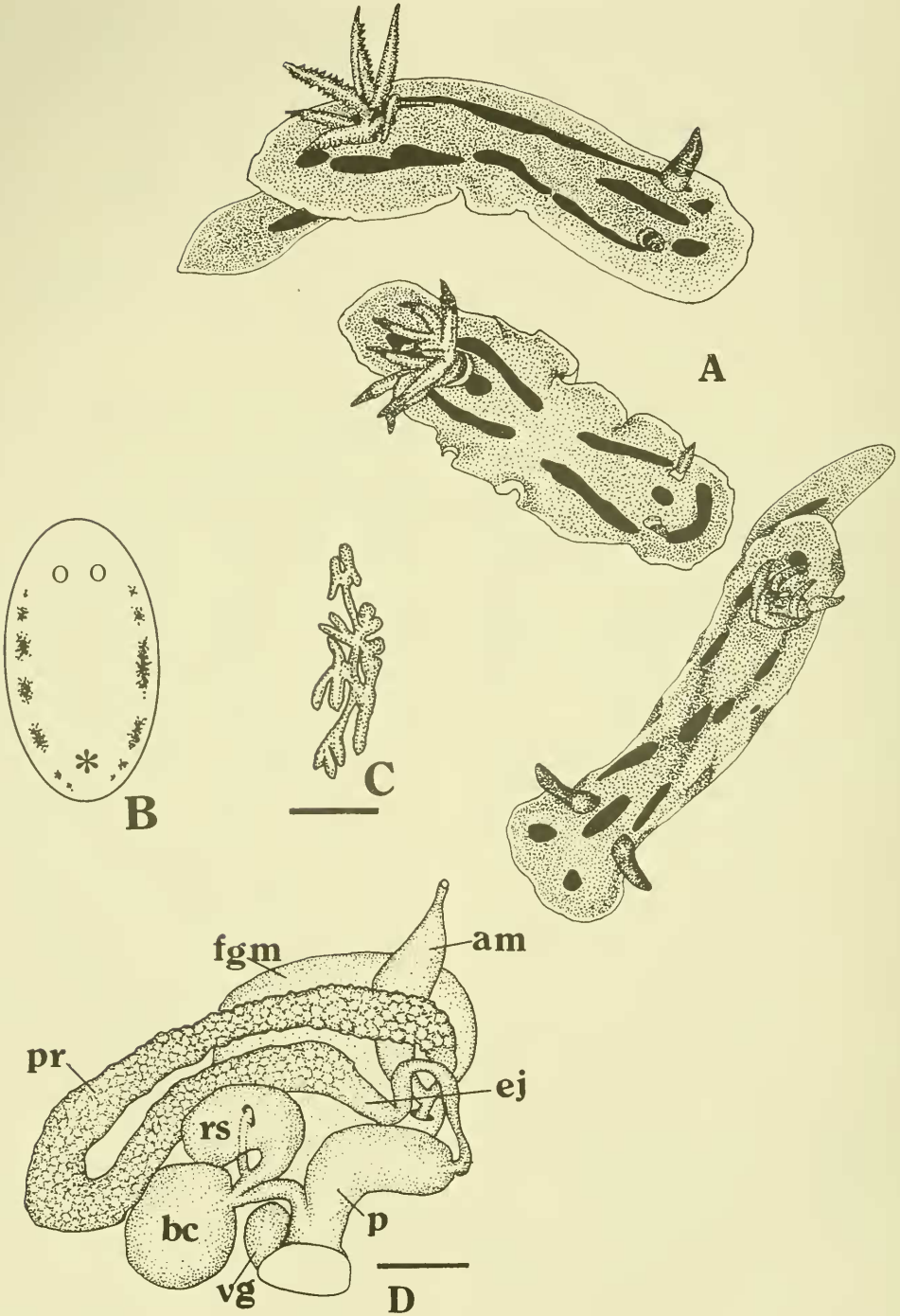


FIGURE 5. *Chromodoris diana* sp. nov. A. Living animals. B. Subcutaneous glandular network. C. Mantle glands, enlarged, scale = 1.0 mm. D. Reproductive system, am = ampulla, bc = bursa copulatrix, ej = ejaculatory duct, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, vg = vestibular gland, scale = 1.0 mm.

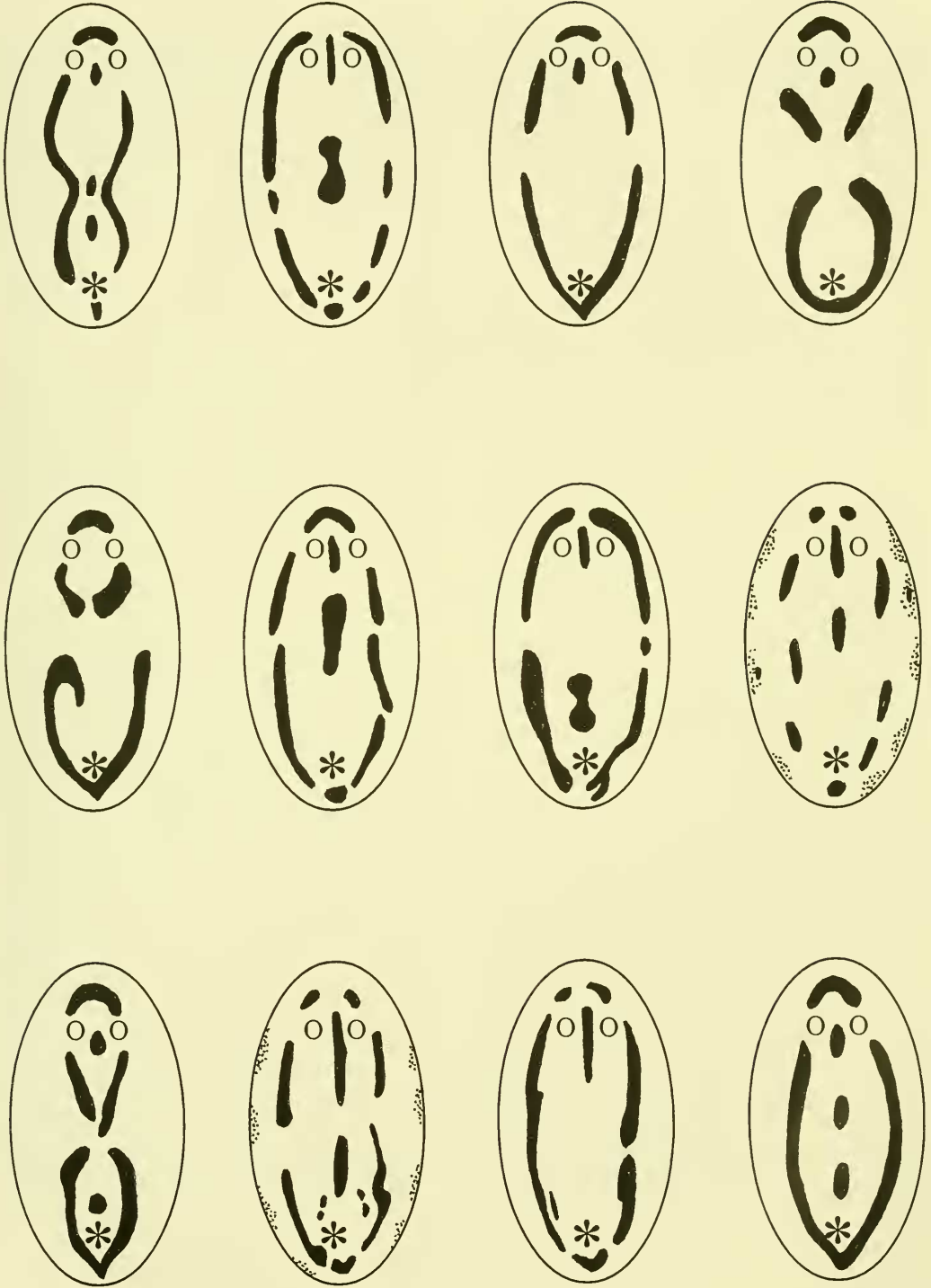


FIGURE 6. *Chromodoris diana* sp. nov. Variation in color pattern.

one specimen, Santa Rosa Island, Cebu, Philippine Islands, 30 m depth, 26 April 1997, D. W. Behrens.

ETYMOLOGY. — *Chromodoris diana* is named for the second author's wife, Diana Lynn Behrens, for her unselfish support and patience with this author during his studies of this group of animals.

DISTRIBUTION. — Thus far, this species is known only from the Philippines and Indonesia, and from photographs by Marc Chamberlain from Sipadan Island, Borneo, Malaysia.

NATURAL HISTORY. — *Chromodoris diana* has commonly been found on relatively shallow walls and reef edges near drop-offs in 10–30 meters depth.

EXTERNAL MORPHOLOGY. — The living animals (Figs. 1B, C) are up to 60 mm in length. The body appears powdery blue due to a fine encrusting of white over blue ground color. Around the margin of the notum is a line of fine, opaque white spots, which are continuous in most specimens examined. A few specimens have a series of orange spots along the margin of the notum, within the boundaries of the white line. Adjacent to the white margin is an area of speckled powdery blue. A discontinuous black submarginal band encircles the medial area of the notum from in front of the rhinophores to behind the gill circle. Black oval spots or patches may occur down the midline of the notum. Patterns of the submarginal band and the spots are highly variable (Figs. 5A, 6). The submarginal band may be nearly entire except for the areas adjacent and lateral to the rhinophores or may be a series of spots and dashes. The width and shape of the submarginal band are variable, as well. When thickening of the band occurs it is usually at the middle of the animal. Towards the middle of the animal, the band may occur closer to the longitudinal midline. All specimens seen have a spot or line between the rhinophores. Posteriorly, the two black submarginal bands may meet behind the gills or may be interrupted with a medial black spot posterior to the gills. Some specimens have two black oval spots down the midline of the notum which either occur singly or directly adjacent to each other forming an hourglass shape. The rhinophores are usually uniformly orange throughout. In one specimen, the upper 2/3 of the rhinophores is orange while the lower 1/3 is transparent. Gills are white, tinged with orange.

Orange coloration may be limited to the longitudinal edges of the gills or may color the upper 1/3 to 1/2 of the gills. A single specimen has black pigmentation along the inner edges of the gills and a smudge of color basally. The hyponotum is similar in color to the notum, with a white marginal line and black submarginal band encircling the posterior end of the foot. This band may be continuous or broken at the junction on the tail.

The subcutaneous mantle glands (Figs. 4E, 5B) form a discontinuous submarginal band around the notum of the animal. Generally, they are absent from the anterior portion of the animal to just behind the rhinophores, but are occasionally situated alongside the rhinophores. These glands are elongate, wide and highly ramified (Fig. 5C). The glands situated near the middle of the body are wider and longer than those located at the anterior and posterior end of the body.

On either side of the head is a short, digitiform oral tentacle. The branchial plume consists of 9–14 unipinnate gills in four specimens examined. The rhinophores are perfoliate with 16–22 simple lamellae.

BUCCAL ARMATURE. — The muscular portion of the buccal mass is approximately equal in length to the oral tube. At the anterior end of the muscular portion of the buccal mass is the chitinous labial cuticle, which bears numerous jaw rodlets. The rodlets (Fig. 7A) are elongate and sharply curved with a deeply bifid apex. The radular formula is 76×47.147 and 71×52.152 in two specimens examined (CASIZ 083684 and 110466, respectively). The vestigial rachidian teeth (Fig. 7B) are long and thin. The innermost lateral teeth (Fig. 7B) are arched with an elongate cusp. There are 2–3 strong denticles on the inner side of the tooth and three denticles on the outer side. The inner denticles are two to three times wider and more rounded than the outer denticles which taper to a sharper point. The second lateral has 3–4 denticles on its outer side. The lateral teeth from the middle of the radular row (Fig. 7C) are elongate and sharply curved with four to five elongate, triangular denticles on the outer side of the teeth. The outermost lateral teeth (Fig. 7D) are elongate with 3–5 finger-like denticles.

REPRODUCTIVE SYSTEM. — (Fig. 5D) The ampulla is short, thick and tubular, narrowing somewhat before bifurcating into an oviduct and vas deferens. The short oviduct enters the female

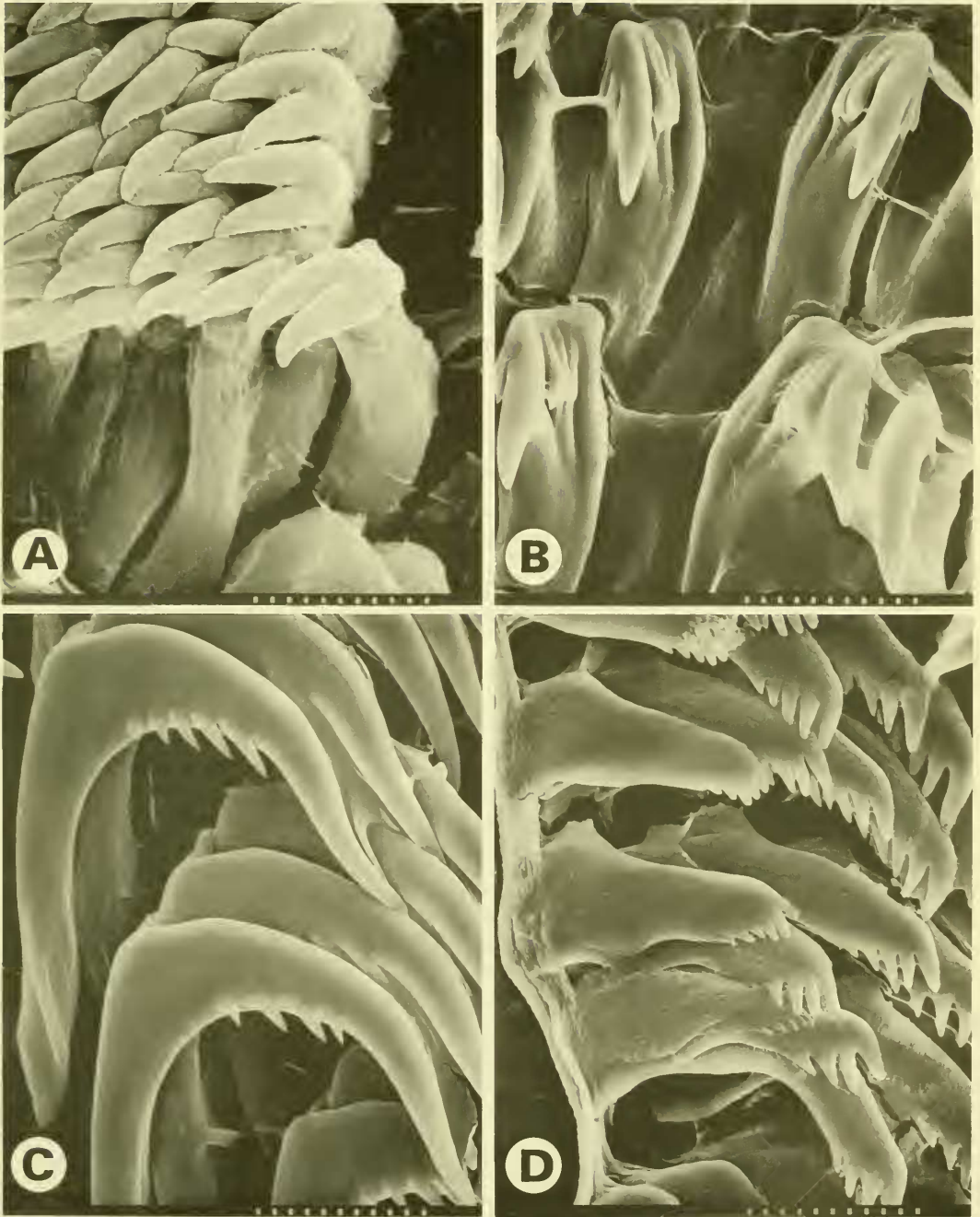


FIGURE 7. *Chromodoris diana* sp. nov. Scanning electron micrographs. A. Jaw rodlets, scale = 7.5 μ m. B. Inner lateral teeth, scale = 20 μ m. C. Lateral teeth from central portion of half-row, scale = 20 μ m. D. Outer lateral teeth, scale = 30 μ m.

gland mass near the albumen gland. The proximal prostatic portion of the vas deferens is folded over itself once before it narrows slightly into the short, muscular, ejaculatory portion. The ejaculatory portion narrows gradually to a curved segment and then enters the elongate penial bulb. The penis is adjacent to the slender vaginal duct at the common gonopore. The distal end of the vas deferens is devoid of any penial hooks. The female gland mass consists of the large mucous gland and smaller membrane and albumen glands. Near the exit of the mucous gland is a small, ovoid vestibular gland. The vagina is relatively short. At the proximal end of the vagina is a short duct to the pyriform receptaculum seminis. The thin walled, spherical bursa copulatrix connects directly to the junction of the proximal end of the vagina and the receptaculum seminis. The uterine duct emerges at a position immediately proximal of the junction of the receptaculum with the bursa and vagina. The uterine duct is relatively short and enters the female gland mass near the albumen gland.

DISCUSSION. — *Chromodoris diana*e is similar in color to other pale blue members of the *Chromodoris quadricolor* complex that lack an orange marginal band. *Chromodoris lochi* Rudman, 1982 and *C. boucheti* Rudman, 1982 have a narrow, continuous submarginal black band and a divided or continuous black longitudinal line along the mid-dorsum. In *C. diana*e, the submarginal band is wider and has large areas where it is interrupted laterally, anteriorly and posteriorly. The mid-dorsal pigment is restricted to a few isolated spots or bands. *Chromodoris willani* Rudman, 1982 also has a continuous submarginal band and a more or less continuous mid-dorsal longitudinal line. It also has gray rhinophores and gills with opaque white spots while those of *C. diana*e are orange and white. *Chromodoris diana*e may have orange spots along the margin of the mantle; the spots are never present in the other three light blue species. The mantle glands of *Chromodoris diana*e are well separated from each other and are highly ramified with digitate branches. Similar mantle glands are found in *C. lochi* and *C. willani* (Fig. 4F, G), but in these two species the glands are less branched, especially in *C. lochi*, where they form compact spherical bodies. Mantle glands are not known for *C. boucheti*.

The radula of *C. diana*e contains 71–76 rows of radular teeth with 47–52 lateral teeth per side. This is similar to the formulae for *C. lochi* and *C. willani* (Rudman 1982). In contrast, *C. boucheti* has 53–56 rows of teeth with only 40–41 lateral teeth per side. The most significant difference in the radula of these four species is the prominent, well-developed rachidian found in *C. willani* (Rudman 1982, fig. 7A, B), while in the remaining species the rachidian is a low, vestigial plate. It appears that the lateral teeth from the middle of the radular row of *C. diana*e are less highly arched and have a more elongate cusp than is depicted for *C. lochi*, *C. boucheti* or *C. willani* by Rudman (1982). In *C. diana*e and *C. willani* there are a maximum of 5 denticles on the middle lateral teeth, while in *C. boucheti* and *C. lochi* there may be as many as 8 denticles.

The reproductive system of *C. diana*e has an extremely short ejaculatory segment of the vas deferens. The reproductive systems of *C. willani* and *C. lochi* were not described in detail, but specimens of these two species were examined here (CASIZ 083679 and 076101, respectively). In both of these species the ejaculatory segment and vaginal duct are proportionately longer than that observed for *C. diana*e and *C. boucheti* (Rudman 1984:136, fig. 13A). The penial bulb of *C. boucheti* is much narrower than the bulbous bulb of *C. diana*e.

***Chromodoris michaeli* sp. nov.**

(Figs. 4I, 8A, 9A–B, 10, 11A–D)

Chromodoris sp. Colin and Arneson, 1995:183, fig. 855.

TYPE MATERIAL. — Holotype: CASIZ 076692, one specimen, Sepok, Maricaban Island, Philippine Islands, 22 m depth, 26 February 1995, Michael T. Ghiselin. Paratypes: CASIZ 079447, one specimen, buccal mass removed, Philippine Islands. CASIZ 085983, one specimen, dissected, unnamed island 20 mi N of Dakak Resort (Mindanao), Philippine Islands, 17–22 m depth, 30 March 1993, T. M. Gosliner. CASIZ 110426, one specimen, Ligpo Island, Balayan Bay, Luzon, Philippine Islands, 20 m depth, 23 April 1997, Bruce Baker. CASIZ 110777, one specimen, Kirby's Rock, Caban Island, Maricaban Strait, Philippine Islands, 20 m depth, 22 April 1997, Bruce Baker.

ETYMOLOGY. — *Chromodoris michaeli* is named for the second author's son, Michael



FIGURE 8. Living animals. A. *Chromodoris michaeli* sp. nov., specimen from Liuay Rock, Dakak, Mindanao, Philippine Islands, photograph by T. M. Gosliner. B. *Chromodoris hintuanensis* sp. nov., specimen from Bus Stop Reef, Balayan Bay, Luzon, Philippine Islands, photograph by T. M. Gosliner. C. *Chromodoris roboi* sp. nov., specimen from Onna Village, Okinawa, Ryukyu Islands, Japan, photograph by Robert Bolland.

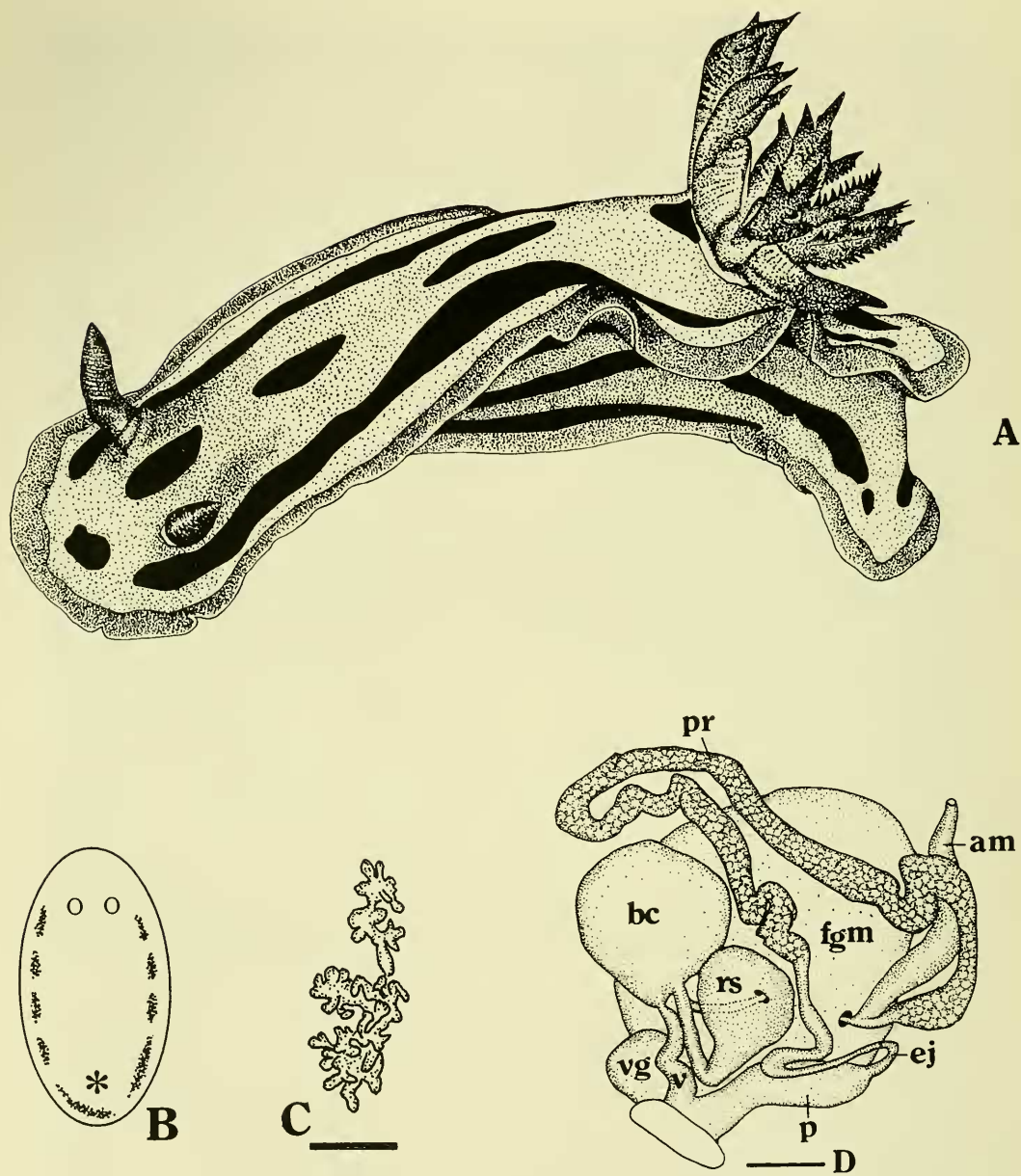


FIGURE 9. *Chromodoris michaeli* sp. nov. A. Living animal. B. Subcutaneous glandular network. C. Mantle glands, enlarged, scale = 1.0 mm. D. Reproductive system, am = ampulla, bc = bursa copulatrix, ej = ejaculatory duct, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vg = vestibular gland, scale = 1.0 mm.

David Behrens, an aspiring biologist with keen interests in malacology.

DISTRIBUTION. — Thus far, this species is known only from three localities in the Philippine Islands: northern Mindanao; Mactan Island, Cebu; and Batangas Province, Luzon (Colin and Arneson 1995; present study).

NATURAL HISTORY. — *Chromodoris michaeli* is found on reef surfaces to a depth of 22 m. We have no information on this species' prey or other habits.

EXTERNAL MORPHOLOGY. — Preserved animals are 24–46 mm in length. The body of the living animal (Figs. 8A, 9A) appears powdery

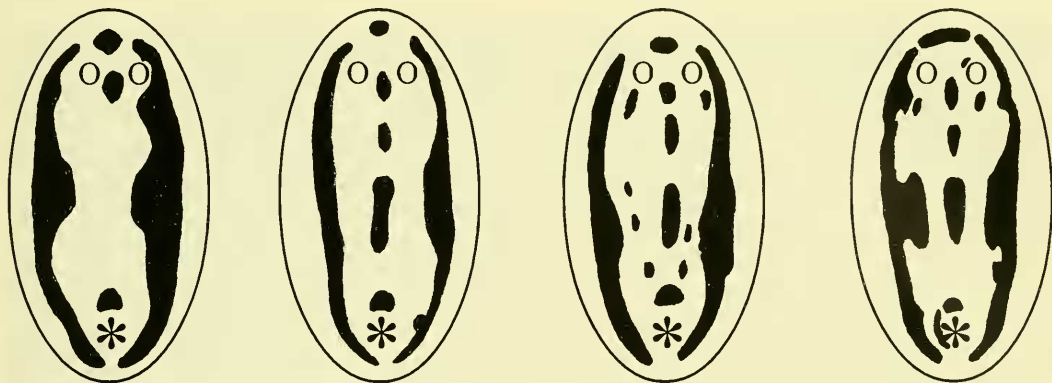


FIGURE 10. *Chromodoris michaeli* sp. nov. Variation of color pattern.

blue due to a fine speckling of white over its blue-brown ground color. A white line edges the margin. Inside the white line is a wide submarginal bright orange band which is uninterrupted. Adjacent to the orange band is a narrow band of pale body color. Inside this blue area is a black band that encircles the animal well posterior to the gills and anterior to the rhinophores. This black band is discontinuous in two spots, submedially at the anterior end and again posteriorly in all specimens seen. Often the band is wider towards the middle. Within the boundaries of this black band are black spots which vary in size, number and position on the notum. One paratype specimen has elongate spots along the midline of the dorsal surface of the notum appearing as a broken line. Additionally, this specimen has random spots. Another specimen has two short longitudinal stripes on either side of the midline at the middle of the animal, spots circling the gills and two elongate spots antero-medially which form a broken line. The specimen depicted by Colin and Arneson (1995, fig. 855) has two spots: one at the base of the gill circle and another between the rhinophores. In some specimens, the black patterns have thin white margins. The range of variation in color pattern is shown in Figure 10. The edge of the foot is orange and the hyponotum is powdery blue with three lateral black stripes in all specimens observed. The gills and rhinophores are burnt orange throughout. The triangular foot extends posteriorly beyond the notum when the animal is crawling.

The subcutaneous mantle glands form a discontinuous submarginal band around the notum of the animal (Figs. 4I, 9B). Glands are densely lobed and convoluted (Fig. 9C) and are generally

absent anteriorly from just behind the rhinophores but occasionally may occur lateral to one or both rhinophores.

On either side of the head is a short, digitiform oral tentacle. In the three specimens examined there are 11–18 unipinnate gills forming the branchial plume. The perfoliate rhinophores bear 21–23 lamellae for the same three specimens.

BUCCAL ARMATURE. — At the anterior end of the muscular portion of the buccal mass is the chitinous labial cuticle, which bears numerous jaw rodlets. The rodlets (Fig. 11A) are elongate, sharply curved and deeply bifid at the apex. The radular formula is $75 \times 61.1.61$ in one specimen examined (CASIZ 079447) and $75 \times 49-51.1.49-51$ in another (CASIZ 085983). The vestigial rachidian teeth (Fig. 11B) are long and thin. The innermost lateral teeth (Fig. 11B) are arched with an elongate cusp. There are two to three prominent denticles on the inner side of the tooth and three to four on the outer side which are bluntly pointed. The inner denticles are two to three times wider than the outer denticles and are more rounded. The lateral teeth from the middle of the radular row (Fig. 11C) are elongate and sharply curved with two to four small, sharply pointed triangular denticles on the outer side of the cusp. Near the base of the denticles the denticle widens abruptly, creating an uneven taper. This is consistent in the two specimens examined. There are no denticles on the inner side. The cusp of the outermost lateral teeth (Fig. 11D) is reduced and bears 4–6 finger-like denticles on the outer side of the teeth.

REPRODUCTIVE SYSTEM. — (Fig. 9D) The ampulla is short, thick and tubular, narrowing somewhat before bifurcating into an oviduct and

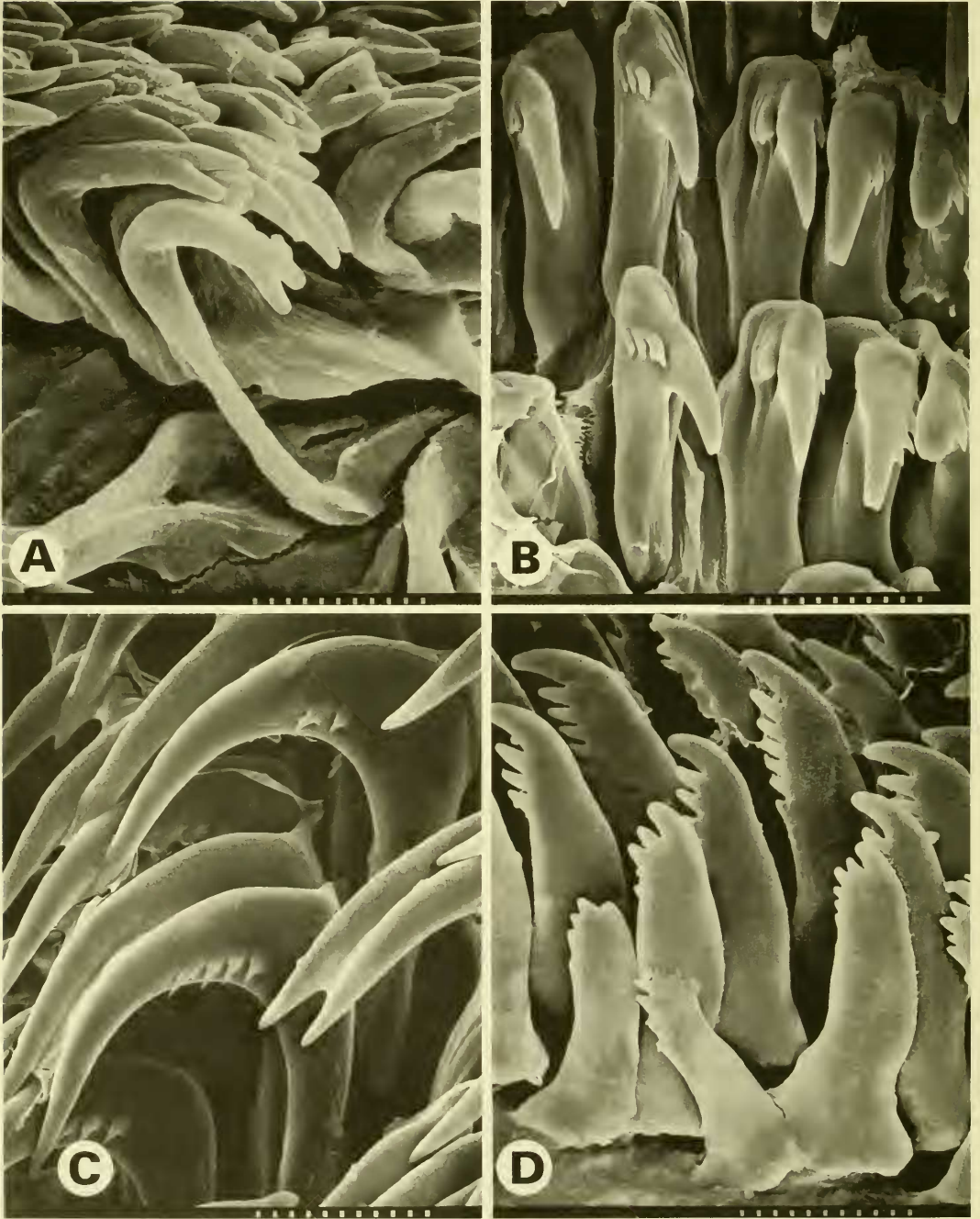


FIGURE 11. *Chromodoris michaeli* sp. nov. Scanning electron micrographs. A. Jaw rodlets, scale = 10 μ m. B. Inner lateral teeth, scale = 30 μ m. C. Lateral teeth from central portion of half-row, scale = 25 μ m. D. Outer lateral teeth, scale = 30 μ m.

vas deferens. The short oviduct enters the female gland mass near the albumen gland. The proximal prostatic portion of the vas deferens is folded over itself once before it narrows markedly into the short, muscular, ejaculatory portion. The ejaculatory portion narrows abruptly to a thin curved segment and then enters the elongate penial bulb. The distal end of the vas deferens is devoid of any penial hooks. The penial bulb is adjacent to the slender vaginal duct at the common gonopore. The female gland mass consists of the large mucous gland and smaller membrane and albumen glands. Near the exit of the mucous gland is a small, ovoid vestibular gland. A relatively short vagina leads to the thin-walled, spherical bursa copulatrix. A short duct emerges from the bursa copulatrix a short distance from its junction with the vagina and connects to the pyriform receptaculum seminis. The uterine duct emerges a quarter of the length along the duct to the receptaculum seminis. The uterine duct is relatively short and enters the female gland mass near the albumen gland.

DISCUSSION. — The color pattern of *C. michaeli* is similar to *C. elisabethina* Bergh, 1877; *C. hamiltoni* Rudman, 1977; *C. quadricolor* (Rüppell and Leuckart, 1828); *C. annae* Bergh, 1877; and *C. westralensis* (O'Donoghue 1924). All of these species have a light blue body color with an orange marginal or submarginal band and black pigment on the body. The first three of these similar species have a continuous black medial line and may have additional black markings on the notum. *Chromodoris westralensis* can be readily distinguished from *C. michaeli* and *C. annae* by the presence of a broad, black medial blotch that connects with the two lateral margins of the black ring. *Chromodoris annae* has dark black pigment spots that show through gaps in the blue-colored area, while in *C. michaeli* these spots are whitish. The blue pigment of *C. michaeli* is lighter than that of *C. annae*. The black submarginal band of *C. annae* is almost always continuous posteriorly, although Rudman (1982, fig. 13E) illustrated a specimen where the lines did not meet posteriorly. In *C. annae* the black bands do not meet anteriorly, but a single black spot is present anteriorly and may extend posteriorly between the rhinophores as an uninterrupted medial line. In *C. michaeli* the anterior portion of the bands is interrupted and a medial anterior black spot is

always present. This spot never extends posteriorly as a line. A second spot is present between or immediately posterior to the rhinophores. Additional black spots or interrupted black bars are usually present on the medial line of the notum. An additional black spot is always present anterior to the anterior margin of the branchial pocket.

The mantle glands of *C. michaeli*, *C. elisabethina*, *C. hamiltoni*, *C. quadricolor*, and *C. annae* are all similar in degree of branching and the fact that the glands are widely separated with approximately 5 glands on either side of the mantle margin.

The radular teeth of *C. michaeli*, *C. elisabethina*, *C. hamiltoni*, *C. quadricolor*, *C. annae* and *C. westralensis* are similar in many respects. All species have a vestigial rachidian tooth. The remaining teeth are all denticulate. In *C. westralensis* there are more radular rows and more teeth per half row than has been reported for the other species (Rudman 1982). The middle lateral teeth of *C. michaeli* have a maximum of four denticles, while *C. hamiltoni* has 4–5 denticles and the remaining species have 6–8.

The reproductive system is similar in its arrangement in *C. michaeli*, *C. elisabethina*, *C. hamiltoni* and *C. annae* (Rudman 1977; present study). It has not been described for *C. quadricolor* or *C. westralensis*. In all cases, the ejaculatory portion of the vas deferens is short relative to most other described chromodorids. In *C. elisabethina* and *C. hamiltoni* (Rudman 1977, fig. 17B, D), the ejaculatory portion is longer than that found in *C. michaeli* and *C. annae* (present study). The vagina of *C. annae* is wider and more elongate than that found in *C. michaeli*.

While only minor anatomical differences separate *C. michaeli* from other blue chromodorids with an orange submarginal band, the differences in coloration, radular tooth morphology and arrangement of reproductive organs are consistent and warrant its consideration as a distinct species.

***Chromodoris hintuanensis* sp. nov.**
(Figs. 8B, 12A–D, 13A–D)

Chromodoris geometrica Debelius, 1996:210, bottom left photograph, not Risbec, 1928, misidentification.

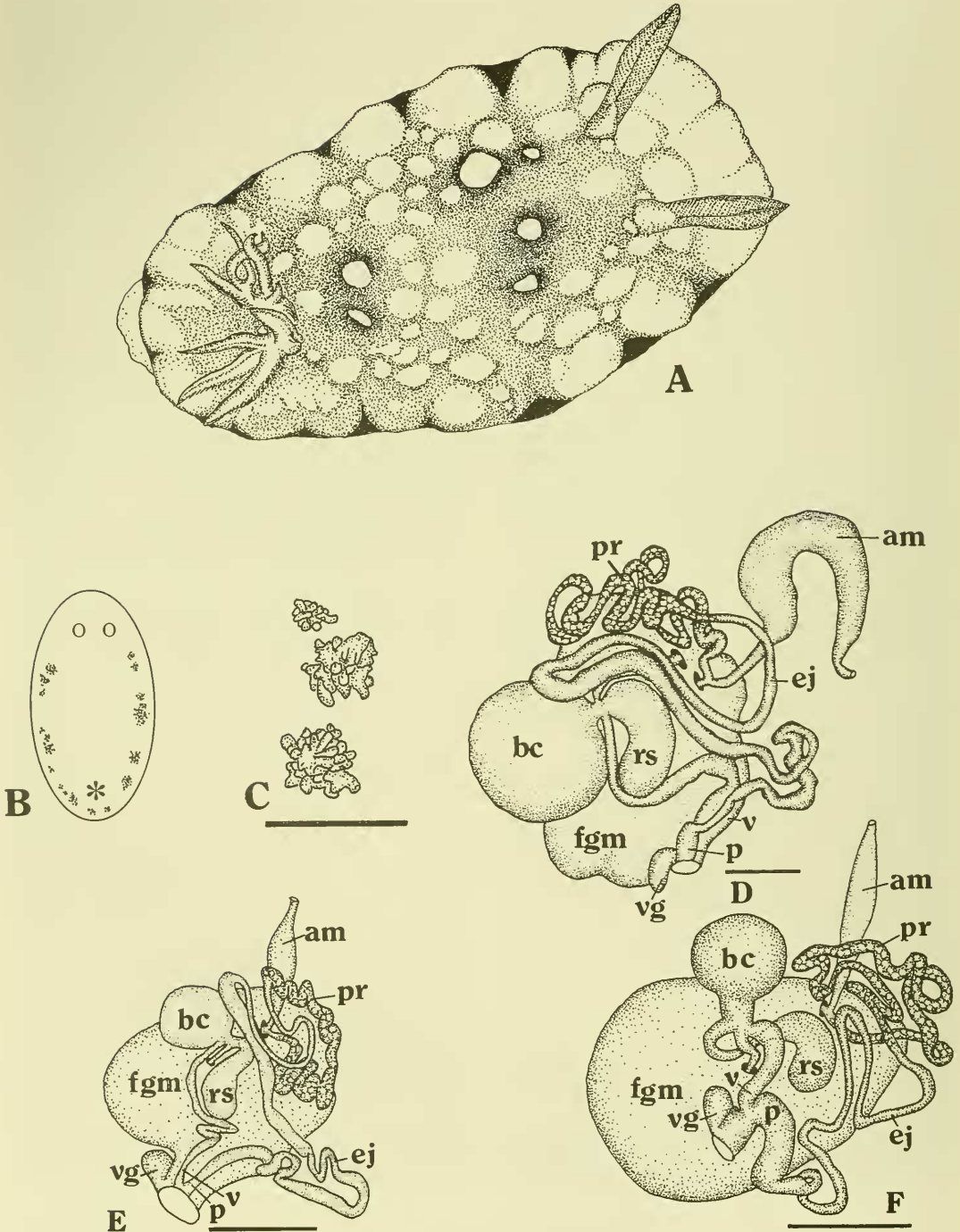


FIGURE 12. A–D, *Chromodoris hintuanensis* sp. nov. A. Living animal. B. Subcutaneous glandular network. C. Mantle glands, enlarged, scale = 1.0 mm. D. Reproductive system, scale = 1.0 mm. E. *Chromodoris geometrica* Risbec, 1928, reproductive system, scale = 1.0 mm. F. *Chromodoris conchyliata* Yonow, 1984, reproductive system, scale = 1.0 mm, am = ampulla, bc = bursa copulatrix, ej = ejaculatory duct, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vg = vestibular gland.

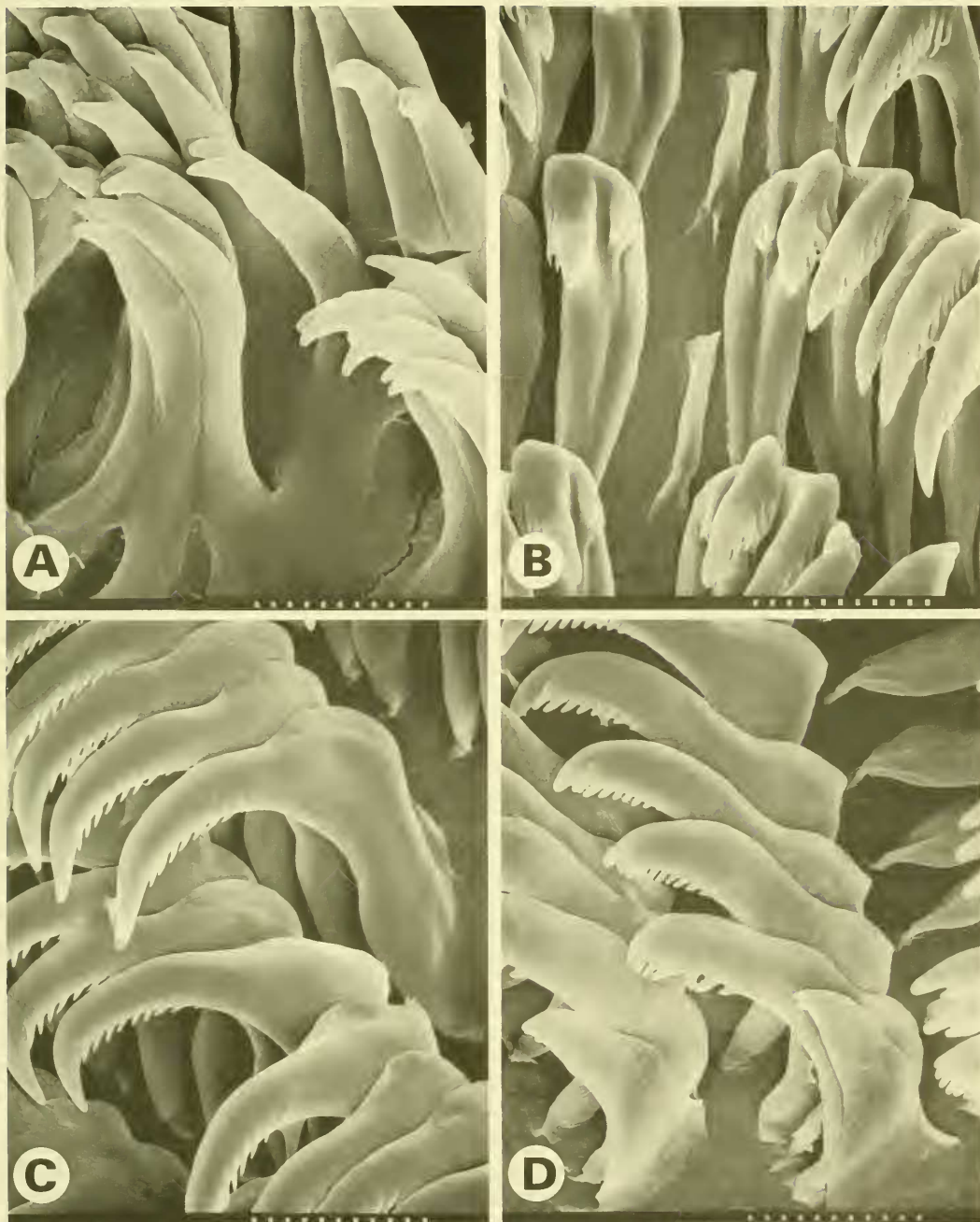


FIGURE 13. *Chromodoris hintuanensis* sp. nov. Scanning electron micrographs. A. Jaw rodlets, scale = 10 μm . B. Rachidian and inner lateral teeth, scale = 25 μm . C. Lateral teeth from central portion of half-row, scale = 30 μm . D. Outer lateral teeth, scale = 30 μm .

TYPE MATERIAL. — Holotype: CASIZ 106491, one specimen, Bus Stop Reef, Balayan Bay, Luzon, Philippine Islands, 2 m depth, 18 April 1996, M. Miller. Paratypes: CASIZ 079286, one specimen, buccal mass removed, Seragaki Beach, 1.3 km ENE of Maeki-zaki, Okinawa, Ryukyu Islands, Japan, 8 m depth, 7 April 1990, Robert F. Bolland. CASIZ 085931, one specimen, Cathedral, Balayan Bay, Luzon, Philippine Islands, 8 m depth, 25 March 1993, T. M. Gosliner. CASIZ 083663, four specimens, one specimen dissected, Bus Stop Reef, Balayan Bay, Luzon, Philippine Islands, 2 m depth, 21 February 1992, T. M. Gosliner. CASIZ 105728, one specimen, Seafari Beach, Anilao, Batangas Province, Luzon, Philippine Islands, 10 m depth, 23 February 1995, M. Miller. CASIZ 103717, one specimen, La Laguna Munbi (point W of Sabang Point), Sabang, Mindoro, Philippine Islands, 1 March 1995, Mel Segara.

ETYMOLOGY. — The name *hintuanensis* comes from the Tagalog word *hintuan* meaning “stopping place,” referring to the type locality, dubbed Bus Stop by the authors, situated offshore from the waiting shed where the bus stops to collect passengers going to Manila.

DISTRIBUTION. — Thus far this species is known only from Bali, Indonesia (Debelius 1996); a photograph by Jim Black from Papua New Guinea; Batangas Province, Luzon, Philippine Islands (present study); Okinawa, Ryukyu Islands, Japan (present study); and from photographs by Mark Strickland from the Andaman Sea, Thailand.

NATURAL HISTORY. — This species is commonly encountered in shallow subtidal sandy or silty habitats, where it is observed crawling in the open. When actively crawling, the animal alternately raises and lowers the anterior portion of the body.

EXTERNAL MORPHOLOGY. — Preserved animals are 11–16 mm in length. The body color of the living animals (Figs. 8B, 12A) is white and the dorsal surface is covered with irregularly-shaped nodules of varying sizes. The mantle margin is edged with deep violet which, in areas of mantle folding, extends inward from the edge to form small patches of color. Small circles of deep magenta outline 5–8 of the small, opaque white, rounded nodules on the medial area of the dorsal surface of the animal and are also found at the base of the rhinophore sheath and gill plume. The outer edges of the circles fade to a plum color which also forms an irregular network on the notum in the spaces between nodules. The rhino-

phores and gills are a dull plum. Crimson lines are present along the longitudinal edges of the gill plumes and on the rachis and lamellae of the rhinophores. In all of the specimens examined, at least one small, rounded nodule is found on the base of the rhinophoral sheath. The foot is white with a deep violet margin and may extend only slightly beyond the posterior edge of the notum when the animal is crawling. There is a high degree of mantle folding.

The subcutaneous mantle glands (Fig. 12B) form a discontinuous submarginal band around the notum except for the anterior portion of the animal from just behind the rhinophores where they are absent. The glands are relatively small yet dense, forming highly lobate masses (Fig. 12D).

On either side of the head is a short, digitiform oral tentacle. There are 10 unipinnate gills forming the branchial plume. The perfoliate rhinophores bear 28–34 lamellae.

BUCCAL ARMATURE. — At the anterior end of the muscular portion of the buccal mass is the chitinous labial cuticle, which bears numerous jaw rodlets. The rodlets (Fig. 13A) are elongate and curved. There is a distinct narrowing of the rodlets towards the apex which is shallowly bifid. The radular formulae of two specimens examined is 48×43.143 (CASIZ 083663) and 47×42.142 (CASIZ 079286). The rachidian teeth (Fig. 13B) are reasonably well developed. Their width is $1/3$ to $1/2$ that of the first laterals. The innermost lateral teeth (Fig. 13B) have a short, pointed cusp and bear 1–2 rounded denticles on the inner side and 4–5 pointed denticles on the outer side which are elongate and curved. The arched lateral teeth from the middle of the row (Fig. 13C) bear 4–8 elongate pointed denticles on the outer side. The cusp on the outermost lateral teeth (Fig. 13D) is reduced and the teeth bear 2–3 rounded, elongate denticles on the outer side.

REPRODUCTIVE SYSTEM. — (Fig. 12D) The ampulla is thick, long and tubular and narrows into a relatively long postampullary duct prior to bifurcating into the oviduct and vas deferens. The short oviduct enters the female gland mass near the albumen gland. The proximal prostatic portion of the vas deferens is tightly coiled, consisting of several distinct loops. The duct narrows slightly and again expands into the relatively long muscular ejaculatory portion, which terminates at a short, tubular penial bulb. The distal

end of the vas deferens is devoid of any penial hooks. The penial sheath is adjacent to the wide, moderately elongate vaginal duct at the common gonopore. The female gland mass consists of a large mucous gland and smaller membrane and albumen glands. Near the exit of the mucous gland is a small, pyriform, elongate vestibular gland. The vagina is long and curved, being markedly narrower proximally. The thin-walled, spherical bursa copulatrix and the pyriform receptaculum seminis have a common junction at the proximal end of the vagina. The bursa is large, nearly twice the size of the receptaculum and one-third the size of the female gland mass. The uterine duct emerges from the common junction of the vagina, the bursa copulatrix and the receptaculum seminis, and enters the female gland mass near the albumen gland.

DISCUSSION. — *Chromodoris hintuanensis* is a member of a group of species in which the anterior end of the body is rhythmically raised and lowered as the animal crawls. Included in this group of species are *C. geometrica* Risbec, 1928 and *C. conchyliata* Yonow, 1984, which are similar in appearance to *C. hintuanensis*. These three species also have a series of tubercular warts on the notum and a network of darker lines. This similarity has led to confusion of these species. Specimens of *C. conchyliata* have been erroneously attributed to *C. geometrica* (Rudman 1973; Gosliner 1987) and specimens of *C. hintuanensis* have been misidentified as *C. geometrica* (Debelius 1996:210, lower left photograph). *Chromodoris roboi*, described here, also exhibits the characteristic behavior of raising and lowering the head (R. Bolland, pers. comm.). However, it lacks the characteristic network of lines found in the other three species described above.

Owing to this confusion, specimens of all three species were examined in this study. Specimens of *C. conchyliata* from Natal, South Africa (SAM A35449) were examined as was a specimen of *C. geometrica* from the Philippines (CASIZ 103766). The three species differ in several aspects of their external morphology and color pattern. The notum of *C. hintuanensis* has a network of pale plum areas while in *C. geometrica* the network is dark brown to black (Yonow 1994; present study) and in *C. conchyliata* it is deep purple (Rudman 1973; Yonow 1984; Gosliner 1987). In *C. hintuanensis* the rhino-

phores and gills have deep red lines along their rachis as do the rhinophoral lamellae. In *C. conchyliata* the gills have red lines along the rachis, but the rhinophores are uniformly red. In *C. geometrica* the gills and rhinophores are yellowish green with opaque white spots. The mantle margin of *C. hintuanensis* has a distinct purple band with a series of indentations around the edge of the mantle. A purple margin without indentations is found only on the anterior end of the mantle margin of *C. geometrica* and is entirely absent in *C. conchyliata*. *Chromodoris hintuanensis* has opaque white spots, which are absent in the other two species. In the specimens of *C. hintuanensis* examined here there are always 10 gills while in *C. conchyliata* there are 7–10 and in *C. geometrica* there are 5–8. *Chromodoris hintuanensis* has more rhinophoral lamellae (28–34) than has been observed in present or previous records of *C. geometrica* (18–22) or *C. conchyliata* (28–29). The mantle glands of *C. hintuanensis* are highly digitate and well scattered, forming a single row of glands. *Chromodoris conchyliata* has as a single row of glands that are positioned more closely together and are less ramified than in *C. hintuanensis*. In *C. geometrica* the glands are arranged in a double row and only a few are highly ramified.

Internally, there are also differences in the reproductive systems, especially with respect to the length of the vagina and the elaboration of the ejaculatory portion of the vas deferens. In *C. hintuanensis* the vaginal duct is of moderate length, whereas it is elongate and convoluted in *C. geometrica* (Figure 12E) and short and wide in *C. conchyliata* (Figure 12F). In *C. hintuanensis* and *C. geometrica* the receptaculum seminis joins the base of the bursa copulatrix while in *C. conchyliata* the receptaculum joins the vagina slightly more distally from the bursa.

***Chromodoris roboi* sp. nov.**
(Figs. 8C, 14A–D, 15A–D)

Chromodoris sp. Coleman, 1989:35, top photograph.
Hypselodoris vibrata Debelius, 1996:239, bottom photograph, not (Pease, 1860), misidentification.

TYPE MATERIAL. — Holotype: CASIZ 079346, one specimen, Horseshoe Cliffs, 1 km NW of Onna Village, Okinawa, Ryukyu Islands, Japan, 26°30'N, 127°50.9'E, 47 m depth, 31 August 1991, Robert F. Bolland. Paratypes: CASIZ 070184, one specimen,

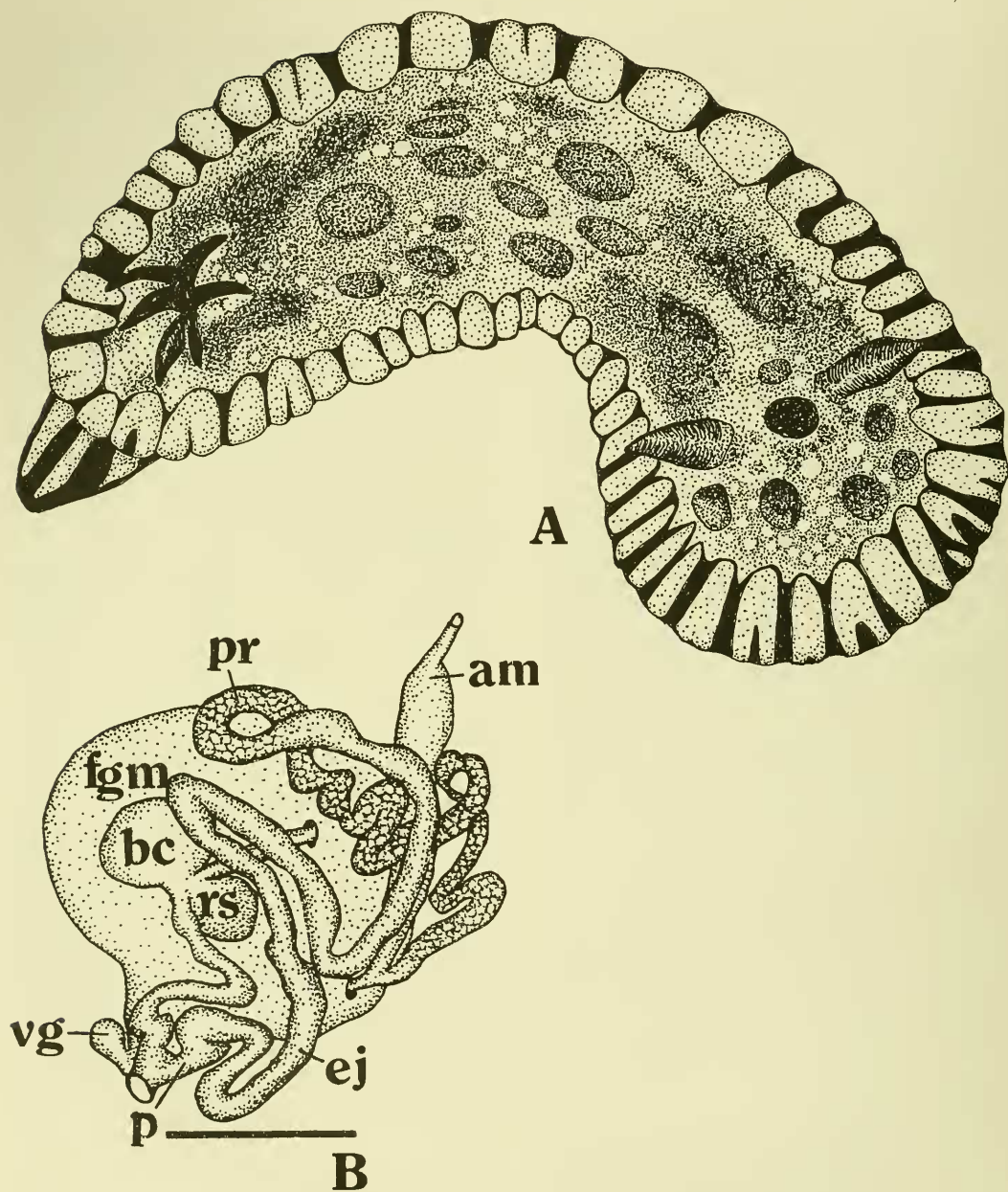


FIGURE 14. *Chromodoris roboi* sp. nov. A. Living animal. B. Reproductive system, am = ampulla, bc = bursa copulatrix, ej = ejaculatory duct, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, vg = vestibular gland, scale = 1.0 mm.

Horseshoe Cliffs, 1 km NW of Onna Village, Okinawa, Ryukyu Islands, Japan, 26°30' N, 127° 50.9' E, 40 m depth, 20 May 1989, Robert F. Bolland. CASIZ 070048, one specimen, Horseshoe Cliffs, 1 km NW of Onna Village, Okinawa, Ryukyu Islands, Japan, 26°30' N, 127°50.9' E, 37 m depth, 1 April 1989, Robert F. Bolland. CASIZ 070120, one specimen,

dissected, Horseshoe Cliffs, 1 km NW of Onna Village, Okinawa, Ryukyu Islands, Japan, 26°30' N, 127°50.9' E, 50 m depth, 11 April 1987, Robert F. Bolland. CASIZ 070230, one specimen, Horseshoe Cliffs, 1 km NW of Onna Village, Okinawa, Ryukyu Islands, Japan, 26°30' N, 127°50.9' E, 50 m feet depth, 9 May 1987, Robert F. Bolland.

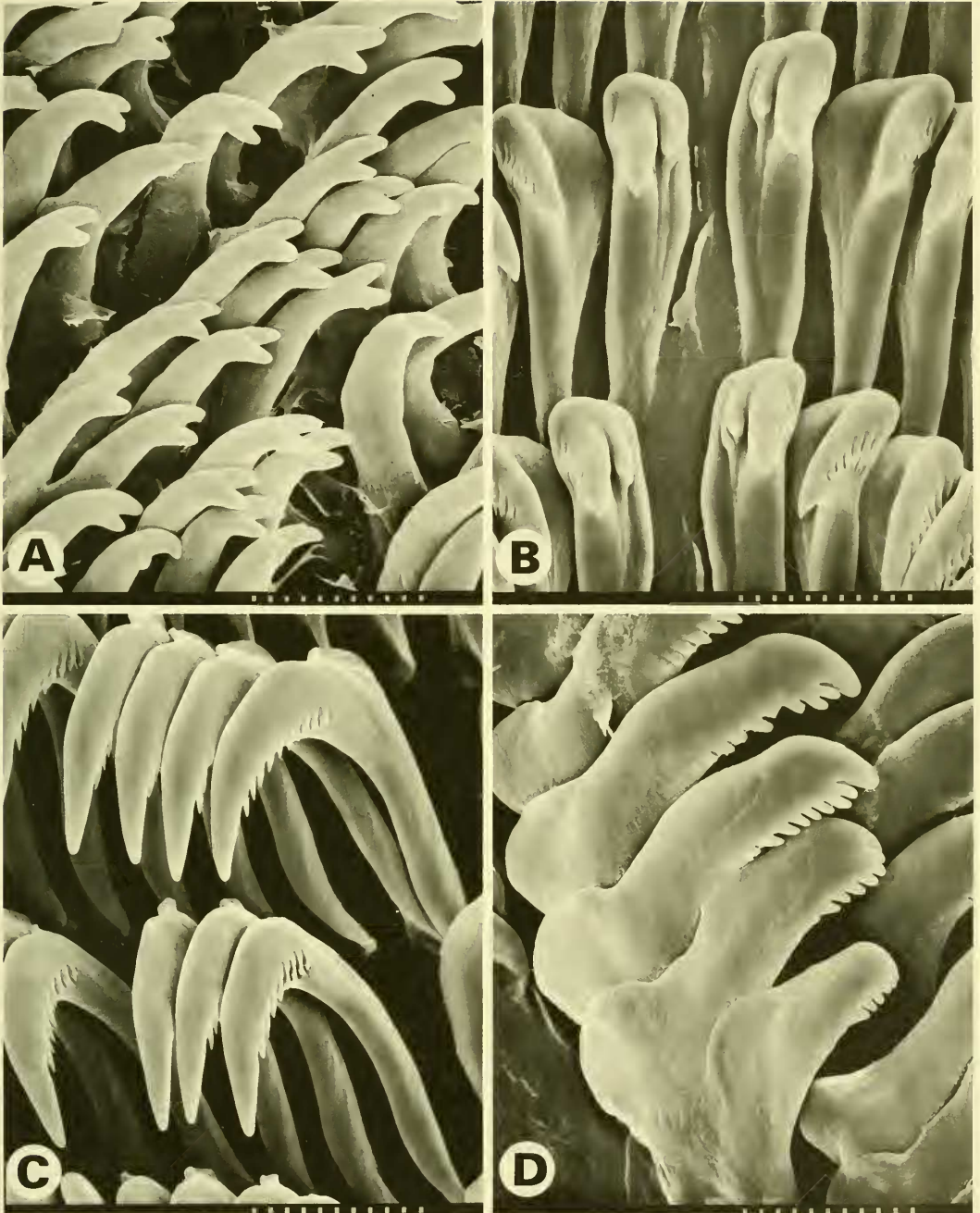


FIGURE 15. *Chromodoris roboi* sp. nov. Scanning electron micrographs. A. Jaw rodlets, scale = 10 μ m. B. Inner lateral teeth, scale = 30 μ m. C. Lateral teeth from central portion of half-row, scale = 30 μ m. D. Outer lateral teeth, scale = 25 μ m.

ETYMOLOGY. — *Chromodoris roboi* is named for Robert Bolland, friend and enthusiastic nudibranch biologist. We have taken the first two letters of his first and last names to produce

“robo,” synonymous with Robo Cop, a fictitious personality equally as daring and adventurous as our friend, Bob Bolland.

DISTRIBUTION. — Thus far this species is known only from Lord Howe Island, New South Wales, Australia (Coleman 1989), Murion Island, Western Australia (Debelius 1996, as *Hypselodoris vibrata*) and Okinawa, Ryukyu Islands, Japan (present study).

NATURAL HISTORY. — As in *C. hintuanensis*, *C. roboi* raises and lowers its anterior end when actively crawling (R. Bolland, pers. comm.).

EXTERNAL MORPHOLOGY. — The living animals (Figs. 8C, 14A) are 17–50 mm in length. This species is easily distinguished by the magnificent, bright blue blocks of color which appear in series separated by black areas of pigment. The blue blocks are squarish or rectangular in shape with edges that are rounded to varying degree. The black color sometimes extends into the outer edges of the blue areas, bisecting them to varying degree. The blue coloration often extends inward from the black marginal band interrupting the yellow-orange pigment which covers most of the notum of the animal. The yellowish orange dorsal surface of the notum is absent in many areas where circles or irregular patches of blue to lavender are visible. These patches are different shapes and sizes. Usually, a large patch is present behind each rhinophore. In some specimens, dark brown blotches cover the dorsal surface to varying degrees. These areas appear wine-colored or black depending on the amount of pigment present. The areas bordering the rhinophore and gill sheaths are orange and may or may not have spots of bright blue, lavender, black or wine color. The lamellae and rachis of the rhinophores and the longitudinal edges of the gill plumes are dark blue to black. In one specimen, the gill plumes are entirely blue-black. Coloration of the foot is similar to that of the mantle margin. It is blue with black stripes radiating from near the median line. There are 5–6 elongate, unipinnate gills and the rhinophores bear 19–22 lamellae.

The mantle margins are very thin and not well preserved in the present material; thus arrangement of mantle glands could not be ascertained. However, it is evident from a photograph of this animal (Debelius 1996:239, lower photograph) that small round mantle glands are arranged in several distinct rows and are found continuously from the posterior end of the animals along the lateral margins to about the level of the rhinophores.

BUCCAL ARMATURE. — The jaw rodlets (Fig. 15A) of the labial cuticle are elongate, curved and shallowly bifid. The radular formulae of two specimens are 50×49.149 and 45×48.148 (CASIZ 070120 and 070184, respectively). The narrow, thin rachidian tooth (Fig. 15B) is elongate at its base. The innermost lateral teeth (Fig. 15B) are curved with a short, pointed cusp. One to two thick, rounded denticles are on the inner side of the tooth and four to five thinner, elongate, pointed teeth are on the outer side. The lateral teeth from the middle of the radular row (Fig. 15C) are arched with an elongate cusp and bear eight to eleven small elongate, pointed denticles on the inner side of the tooth. The cusp of the outermost lateral teeth (Fig. 15D) is reduced and the teeth bear 8–10 finger-like denticles.

REPRODUCTIVE SYSTEM. — (Fig. 14B) The ampulla is thick and tubular, narrowing somewhat before bifurcating into an oviduct and vas deferens. The short oviduct enters the female gland mass near the albumen gland. The proximal prostatic portion of the vas deferens is slender and forms a few tight loops. The relatively long, muscular ejaculatory portion is similar in width to the prostatic portion and terminates in a relatively short penial bulb. The distal end of the vas deferens is devoid of any penial hooks. The penial bulb is adjacent to the slender vaginal duct at the common gonopore. The female gland mass consists of a large mucous gland, and smaller but indistinct membrane and albumen glands. Near the exit of the mucous gland is a small, ovoid vestibular gland. The vagina is relatively long and curved. The thin-walled, spherical bursa copulatrix and the pyriform receptaculum seminis share a common junction at the proximal end of the vagina. The uterine duct emerges from this junction and enters the female gland mass near the albumen gland.

DISCUSSION. — *Chromodoris roboi* is readily distinguishable from all other described species of *Chromodoris* by its unique pattern of coloration. It is the only species with a yellow-orange body color with blue marginal rectangles separated by black spaces. *Chromodoris vibrata* (Pease, 1860) is the most similar species in terms of color pattern and has been confused with *C. roboi* (Debelius 1996:239, lower photograph). It is a yellow-orange animal with white pustules on the notum and a white marginal region with triangular dark blue interrupting the white. It also

has dark blue pigment on the rachis of the gills and on the white rhinophores. *Chromodoris roboi* has 5–6 gills which do not appear to vibrate (R. Bolland, pers. comm.) while *C. vibrata* has 8–10 vibratile gills (Kay and Young 1969, as *Hypselodoris vibrata*).

The radula of *C. roboi* has more rows of teeth than has been described for *C. vibrata*. A specimen of *C. vibrata* with 56 rows of teeth had only 38 teeth per half row (Kay and Young 1969) while a specimen of *C. roboi* with 50 row of teeth had 49 teeth per half row. A vestigial rachidian tooth is present in *C. roboi* but is apparently absent in *C. vibrata*. The lateral teeth from the middle of the radular row of *C. roboi* have 8–11 denticles, while those of *C. vibrata* have a maximum of four denticles.

The reproductive systems of *C. roboi* and *C. vibrata* appear to have some differences, as well. Kay and Young (1969) describe a large curved receptaculum seminis while the specimen of *C. roboi* described here has a small pyriform receptaculum. The ejaculatory portion of the vas deferens of *C. roboi* is much larger than that described for *C. vibrata*. No vestibular gland was described for *C. vibrata*. However, additional material should be examined to verify this observation.

Chromodoris aureopurpurea Collingwood, 1881, also bears some resemblance to *C. roboi* in its coloration. This species has a white body with dark blue intrusions along the mantle margin and orange spots on the notum (Rudman 1987:342, fig. 23B). It also has opaque white lines on the gills and rhinophores, which are absent in *C. roboi*. Its radular formula is more similar to that of *C. roboi* than that of *C. vibrata*. The radular teeth of *C. aureopurpurea* have a smaller rachidian plate and have far coarser, more well separated denticles (Rudman 1987:349, fig. 23) than those present in *C. roboi*. The ejaculatory duct of *C. roboi* is much wider than that depicted for *C. aureopurpurea* (Rudman 1987:351, fig. 29B).

DISCUSSION

Rudman (1982) described several species in the *Chromodoris quadricolor* complex. In this paper he stated that members of this color complex represent an artificial group in a phylogenetic sense, since species of *Hypselodoris* are

also included. Since then, Rudman (1984) has determined many useful characters, such as elaboration of mantle glands, variation in radular morphology and elaboration of the reproductive system, to distinguish between chromodorid genera. However, he questioned the utility of employing several of these characters in the separation of species groups within genera. In examining the species described in the present paper and in comparing them with other taxa, we have observed several consistent anatomical features within *Chromodoris*. The mantle glands within species of the *Chromodoris quadricolor* complex are all relatively large and highly digitate. The species with black and white or yellow pigment (*C. africana*, *C. magnifica* and *C. joshi*) have a more or less continuous band of glands around the margins, although they are more separated in *C. magnifica* than in the other two species examined. Members of this group, including *C. kuiteri* Rudman, 1982, have smaller, reduced denticles on the middle lateral teeth. These facts suggest that the similarities between these species with similar color patterns are not just limited to color, but that they may have closer phylogenetic proximity to each other than to other taxa. Similarly, members of the *C. quadricolor* complex with a blue body color (*C. lochi*, *C. willani*, *C. elisabethina*, *C. annae*, *C. hamiltoni*, *C. diana*e and *C. michaeli*) examined in this study tend to have more highly ramified mantle glands that are well separated from each other. In addition, the reproductive system of all of the species examined here in the *Chromodoris quadricolor* complex (*C. joshi*, *C. diana*e, *C. michaeli*, *C. lochi*, *C. willani* and *C. annae*) plus species previously studied by Rudman (1977) (*C. magnifica*, *C. elisabethina*, *C. africana* and *C. hamiltoni*) and Rudman (1984) (*C. boucheti* and *C. kuiteri*) all have an extremely short ejaculatory segment of the vas deferens. The morphology of the reproductive system of these species differs from other species of *Chromodoris* described here (*C. hintuanensis* and *C. roboi*) which are not part of the *C. quadricolor* complex. These other species have much longer prostatic and ejaculatory portions of the vas deferens. Elongate prostatic and ejaculatory segments are present in most other species of Indo-Pacific *Chromodoris* not included in the *C. quadricolor* complex (Kay and Young 1969; Rudman 1987; Gosliner 1994). Other species from southern

Australia (Rudman 1987) also have a short ejaculatory segment.

Based on the examination of the distribution and arrangement of mantle glands and reproductive characters examined here, there is evidence that the species of *Chromodoris* placed within the *C. quadricolor* color group may represent a distinct subclade within this large genus consisting of several hundred species. Identification of monophyletic subunits is essential in building an understanding of the phylogenetic relationships in order that comparative biological studies of biogeography and evolution of color patterns may be undertaken. Preliminary data with respect to variation in distribution of mantle glands and reproductive characters present promising data to untangle the seemingly overwhelming diversity of *Chromodoris* species and certainly warrant further study of anatomical features to develop a more comprehensive data set for phylogenetic analysis.

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